PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY OF LONDON

PAPERS.

1. The Morphology of the Cyprinodont Fishes of the Subfamily Phallostethinæ, with Descriptions of a new Genus and two new Species. By C. Tate Regan, M.A., F.Z.S.

[Received November 8, 1915: Read November 23, 1915.]

(Plates I.–IV.* and Text-figures 1–15.)

Index.

1. *Introduction.*

In 1913 I described an extraordinary little Cyprinodont fish from Johore, and named it *Phallostethus dunckeri* (Regan, 11). Some more fishes from the same locality have been sent to me

* For explanation of the Plates see p. 25.

for description; they represent a new genus, *Neostethus*, related to *Phallostethus*, and belong to two new species, *N. lankesteri* and *N. bicornis*.

Of *Neostethus lankesteri* there are six specimens, all about 30 mm. in total length; five are adult males and the other is an adult female. They come from the Muar River (brackish-water) and from Singapore. Some features in their structure, such as the number of vertebræ and the general relations of the viscera, have been elucidated by prolonged clearing with oil of cloves, but the detailed account of the structure of the male fish is based on the study of a series of transverse sections. Of *N. bicornis* there are three examples, two males (21 and 25 mm. long)—one immature, the other nearly adult—and a female of 24 mm.; these are from Kuala Langat (brackish-water).

Phallostethus is redescribed and is compared with *Neostethus*.

2. *Structure of Female* Neostethus lankesteri *, *gen. et sp. n.*

a. External Characters.

Form elongate, strongly compressed. Head rather small; mouth terminal, strongly oblique, protractile, with one or two series of conical teeth in the jaws; eyes large, lateral. Scales very similar in structure to those of *Panchax*; 34 to 36 in a longitudinal series. Dorsal fin of 5 or 6 rays, above the end of the rather long anal, which has 15 or 16 rays; caudal emarginate; pectorals 10 or 11-rayed, placed rather high. Anus (text-fig. 12, B, *a.*), genital aperture, and urinary opening behind each other in middle line below bases of pectoral fins; behind them abdomen compressed to an edge bearing a rayless fringe (text-fig. 12, B, *f.*); just behind anus a pair of papillæ (text-fig. 12, B, *p.*) (? vestigial pelvic fins †), one much larger than the other, that partly cover a depression into which the oviduct and ureter open.

b. Skeleton.

The skeleton is typically Cyprinodont and essentially similar to that of *Panchax*, except that the hæmal arches of the caudal vertebræ are not expanded, as the air-bladder does not extend back into the tail. The vertebræ number 34 or 35 (15–16+19).

c. Viscera.

The air-bladder occupies the posterior part of the abdominal cavity; it is large, simple, and thin-walled, except an anterior

* I have ventured to name this species in honour of Sir Ray Lankester, K.C.B., F.R.S., to whom I am indebted for many acts of kindness and much sound advice. Moreover, it seems to me not inappropriate that this little fish, whose structure presents more than one problem for the consideration of students of animal morphology, should bear the name of the most distinguished morphologist of our time.

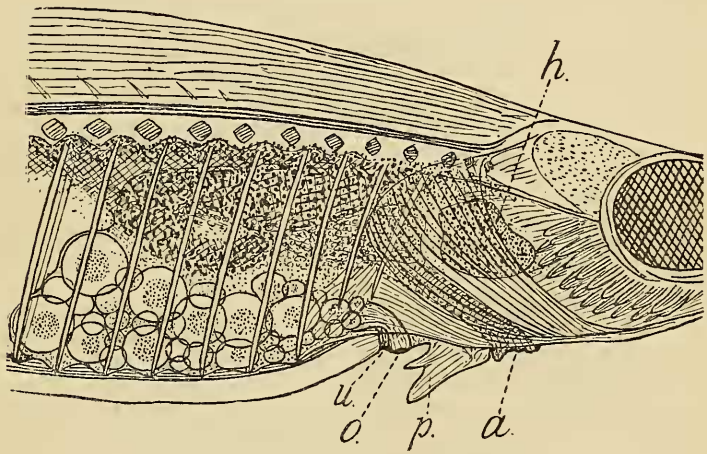
† In *Phallostethus* the postanal papillæ are supported by a pair of minute skeletal elements that may be vestigial pelvic bones.

part, tapering forwards, that has thick glandular walls. There is no trace of a pneumatic duct.

The short œsophagus leads into the stomach, which is simple, without cæcum or pyloric appendages; the intestine forms a single coil just in front of the air-bladder, and then runs downwards and forwards to the anus. The liver is large, and there is a well-developed spleen situated on the anterior part of the intestinal coil.

The kidneys extend from below the basioccipital to the posterior end of the abdominal cavity; they are paired, but not enlarged, anteriorly, unpaired posteriorly; the ureters leave the kidneys

Text-figure 1.



Neostethus lankesteri, ♀. Part of head and abdominal region cleared and viewed as a transparent object (× 10). The ovary is clearly visible, lying in front of the air-bladder and below the alimentary canal.

h., heart; *a.*, anus; *p.*, postanal papillæ; *o.*, opening of the oviduct; *u.*, opening of ureter.

above the anterior part of the air-bladder and soon unite to form a single duct that runs downwards and forwards below the intestine. The ovary is unpaired and lies in front of the air-bladder and below the intestine; it narrows forwards, and the very short oviduct arises from its anterior end. The ova are comparatively few and large.

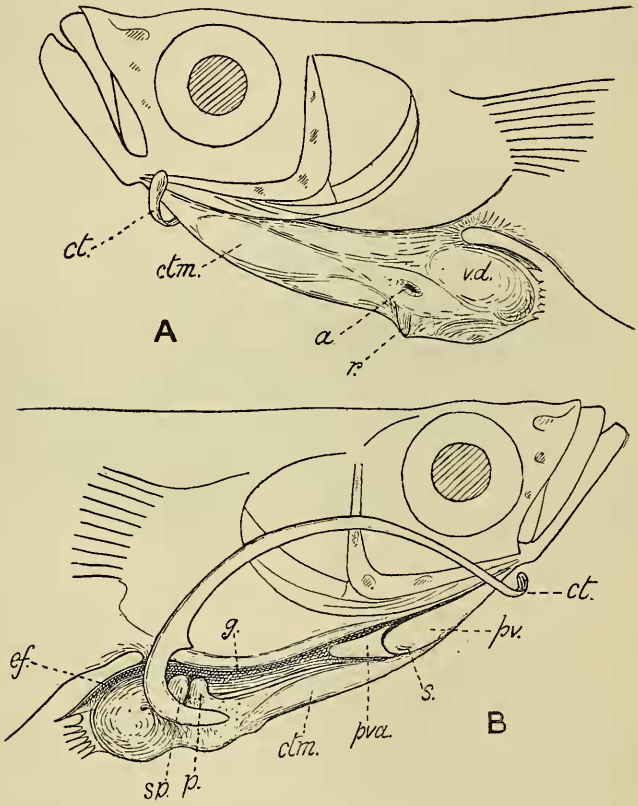
Except for modifications correlated with the thoracic position of the anus and urino-genital apertures, *e. g.* that the air-bladder is posterior instead of superior, the intestine runs forwards instead of backwards, etc., the visceral anatomy is essentially similar to that of the Fundulinæ.

3. *Structure of Male* Neostethus lankesteri.

a. External Characters.

The male differs from the female externally in the presence of the priapium (text-fig. 2), a fleshy appendage that lies below the

Text-figure 2.



Neostethus lankesteri, ♂. Head and priapium (× 10). A, proctal side; B, aproctal side.

ct., ctenactinium; *ctm.*, ctenactinial muscle; *a.*, anus; *r.*, end of priapial rib; *v.d.*, terminal coil of vas deferens; *pv.*, pulvinulus; *pva.*, pulvinular appendage; *s.*, pulvinular spine; *g.*, glandular groove; *ef.*, efferent groove; *sp.*, seminal papilla; *p.*, infrasulcar prominence.

head and the anterior part of the body, to which it is attached for the greater part of its length, only the posterior end being free. Anteriorly the priapium is confluent with the isthmus;

further back it increases in size and is well-defined; owing to a strong constriction of the body just behind its attachment, the posterior part of the priapium projects but little beyond the general outline of the abdominal region.

On one side, the proctal side, which may be either right or left, may be seen the anus (*a.*); above and behind it can be seen the outline of the enlarged terminal coil of the vas deferens (*v.d.*), occupying most of the free posterior part of the priapium, which ends in a membranous fringe, produced into some half-dozen slender processes. On the proctal side a shallow groove marks the boundary between the priapium and the body of the fish, but on the other side, the aproctal side, there is a much deeper groove, margined above by a thick fold of the integument; this groove is lined by a glandular epidermis, and may be termed the glandular groove (*g.*). Posteriorly a dermal fold arises from the inner wall of the groove, and this fold is continued backwards on the free part of the priapium as the roof of another groove, leading from the glandular groove to the end of the priapium; this may be termed the efferent groove (*ef.*).

The enlarged part of the vas deferens lies below the floor of the efferent groove; here it is running backwards, and at the end of the priapium it curves round from the proctal to the aproctal side and then runs upwards and forwards, ending in a seminal papilla (*sp.*), which opens into the glandular groove, the terminal aperture being a wide slit. Directly in front of the seminal papilla is a papilliform projection (*p.*), which may be termed the infrasulcar prominence. Below the infrasulcar prominence is the articulation of the ctenactinium (*ct.*), a long and slender movable bony appendage that curves backwards and upwards, then forwards to below the eye, and, finally, downwards and across beneath the chin; a short pointed process, directed outwards and downwards, arises from its concave edge above the infrasulcar prominence.

Further forwards, a rather soft appendage, subconical in form and with its apex directed backwards, lies in the glandular groove; at its base it is separated by a deep constriction from a lateral mass of tissue that tapers forwards to the anterior end of the priapium. This mass of tissue may be termed the pulvinulus (*pv.*) and its appendage the pulvinular appendage (*pva.*); a small antrorse spine (*s.*) projects from the posterior part of the pulvinulus, and a branch of the glandular groove runs forwards between the priapium proper and the lower part of the pulvinulus; this infrapulvinular groove narrows forwards and disappears a little in advance of the level of the pulvinular spine.

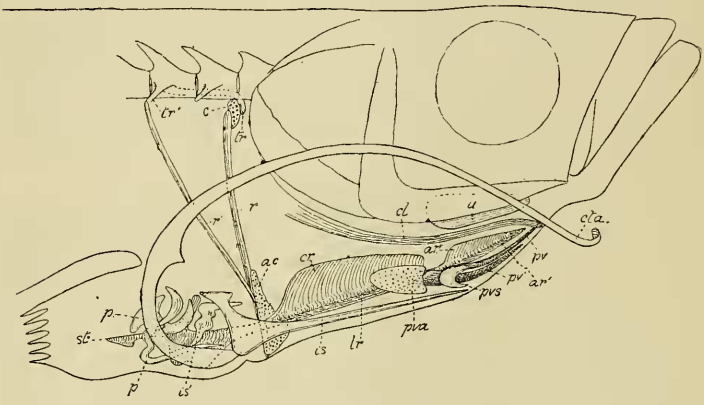
b. Skeleton (Pl. I. B, and text-fig. 3).

This differs from that of the female in that one of the cleithra, the third vertebra, and the first pair of ribs are modified in

connection with the priapium, whilst the priapium itself has a special skeleton.

Cleithra.—The cleithrum of the proctal side is normal and ends anteriorly below the angle of the præoperculum. That of the aproctal side is produced into a slender process (*cl.*) that extends forward to below the attachment of the urohyal; this process lies between the isthmus and the priapium; it is somewhat expanded transversely (Pl. I. A), and anteriorly it spreads downwards on each side of the priapium, almost enclosing it.

Text-figure 3.



Neostethus lankesteri. Skeleton of priapium from the aproctal side (× 12) (diagrammatic).

cta., ctenactinium; *u.*, urohyal; *cl.*, cleithrum; *tr.*, *tr.'*, transverse processes of third vertebra; *c.*, cartilage; *r.*, *r.'*, first pair of ribs; *ac.*, antepleural cartilage; *pva.*, pulvinular appendage; *pvs.*, pulvinular spine; *pv.*, outer, and *pv.'*, inner pulvinular bones; *is.*, anterior, and *is.'*, posterior infrasulcar bones; *p.*, papillary bone; *a.r.*, vertical, and *a.r.'*, horizontal anterior ridges of axial bone: *lr.*, its lateral ridge; *cr.*, its main crest; and *st.*, its terminal style.

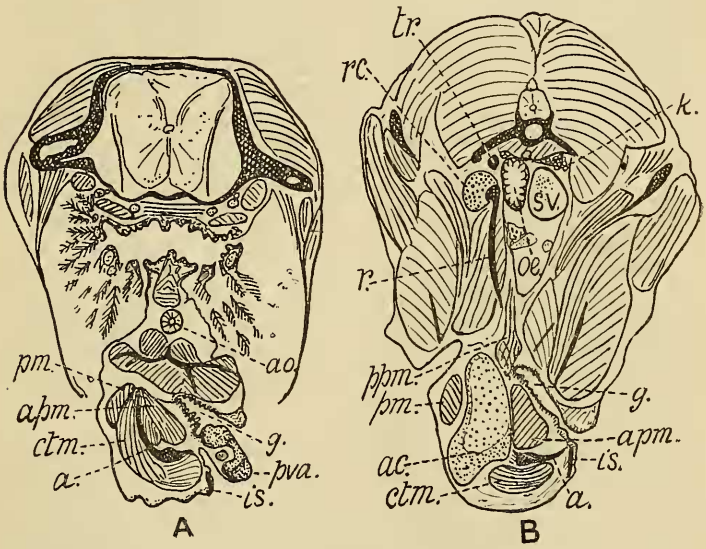
Third vertebra.—The transverse process of the aproctal side (*tr'.*) is normal, but that of the proctal side (*tr.*) is much stronger; proximally it is directed outwards at right angles to the centrum, then it runs forwards below the transverse process of the second vertebra (text-fig. 4 B), until it reaches the level of the first vertebra, when it curves downwards and ends.

First pair of ribs.—These are attached proximally to the transverse processes of the third vertebra; the rib of the aproctal side (*r.'*) is not particularly strong, but it is very long and runs downwards and forwards into the priapium; the rib of the proctal side (*r.*) is much stouter and runs downwards right to the ventral surface of the priapium below the anus (text-fig. 2, *r.*); proximally a nodule of cartilage (*c.*) intervenes

between the end of the rib and the posterior face of the decurved part of the transverse process. A mass of cartilage, the antepleural cartilage (*ap.*), lies in front of the distal ends of this pair of ribs and embraces them laterally; this mass is to a large extent composed of parenchymatous cartilage, but in the centre approaches true hyaline cartilage in structure (*cf.* text-fig. 4, B).

Axial bone of the priapium.—This extends nearly the whole length of the priapium; in front of the articulation of the ctenactinium it has the form of a rod of cartilage enclosed in a cylinder of bone (Pl. III. A, *a.*) that bears certain crests and ridges, namely, (1) the anterior ridges, the upper (*ar.*) vertical, the lower (*ar.'*)

Text-figure 4.



Neostethus lankesteri, ♂. Transverse sections (× 18): A, through postorbital part of head and base of pulvinular appendage; B, through second vertebra and antepleural cartilage.

ao., aorta; *g.*, glandular groove; *pva.*, pulvinular appendage; *a.*, axial bone; *is.*, infrasulcar bone; *ctm.*, ctenactinial muscle; *pm.*, muscle of proctal side; *apm.*, muscles of aproctal side; *ppm.*, pleuro-priapial muscle; *ac.*, antepleural cartilage; *r.*, priapial rib; *rc.*, cartilage; *tr.*, transverse process of third vertebra; *k.*, kidney; *œ.*, œsophagus; *sv.*, sinus venosus.

nearly horizontal and aproctal; these increase in height backwards and end abruptly at the level of the pulvinular spine. (2) The main crest (*cr.*): this rises obliquely from the proctal side of the axial bone and then curves upwards until it is vertical (text-fig. 4 A, *a.*); it commences a little behind the end

of the anterior ridges and ends in front of the priapial ribs. (3) The lateral ridge (*lr.*), on the aproctal side from the level of the end of the pulvinular appendage to the level of the priapial ribs; this ridge almost reaches the surface at the lower margin of the glandular groove. The axial bone passes backwards on the aproctal side of the priapial ribs and antepleural cartilage, and in the region of the anus it becomes stouter and expands downwards; the ctenactinium (*cta.*) is attached to the aproctal side of this part of the axial bone. In the region of the seminal papilla the axial bone extends upwards nearly to the glandular groove, and behind this it contracts to form a terminal style (*st.*) that runs backwards and ends just in front of the transverse portion of the terminal coil of the vas deferens.

Anterior infrasulcar bone (*is.*).—This is a laminar bone that lies near the surface on the aproctal side. It is broad posteriorly and tapers anteriorly; behind it extends from the floor of the glandular groove under the base of the infrasulcar papilla to outside the proximal end of the ctenactinium; for the greater part of its length its upper edge is just below the edge of the lateral ridge of the axial bone; anteriorly it lies within the inner surface of the infrapulvinular groove (Pl. II. B, *is.*) and is quite a slender bone. Near its posterior end, where its lower edge overlaps the end of the ctenactinium, it bears an inner knob to share with the axial bone in supporting that appendage.

Posterior infrasulcar bone (*is.'*).—A bone whose expanded upper surface lies just below the floor of the glandular groove, below the anterior part of the seminal papilla; it is a solid bone that extends downwards and inwards on the aproctal side of the axial bone; from its upper surface it sends forwards a laminar process that runs below the anterior infrasulcar bone into the base of the infrasulcar prominence.

Papillary bone (*p.*).—A bone that supports the seminal papilla, which it enters from behind and below, and then divides into three branches that expand into laminæ lying just below the skin, one on the inner side of the papilla and two, an upper and a lower, on its outer side. Before entering the papilla the bone is a slender rod that curves downwards across nearly to the ctenactinium and then tapers forwards and inwards, ending a little in advance of the seminal papilla on the aproctal side of the axial bone (*cf.* Pl. II. A, and text-fig. 7 A, *p.*).

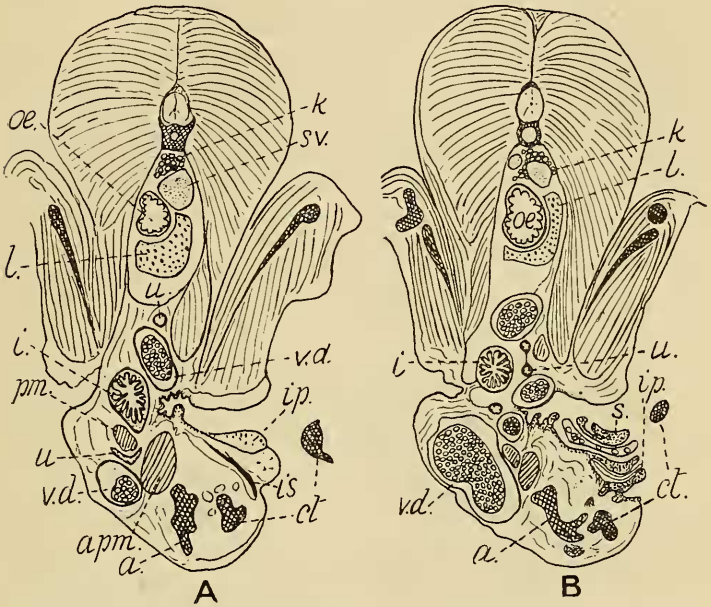
The pulvinular appendage (*pva.*) is subconical, somewhat compressed; it is a mass of parenchymatous cartilage, but has the structure of true hyaline cartilage on the inner side near the base; in this region it is hollowed out for the reception of a cartilaginous peg that arises from a bone in front of it (Pl. II. B).

The pulvinulus consists of fibrous connective tissue surrounding two longitudinal bones, the inner and outer pulvinular bones.

The inner pulvinular bone (*pv.'*) is largest posteriorly, where

it bears a backwardly directed process for the support of the pulvinular appendage; it tapers anteriorly and ends below the axial bone at about the middle of the length of the anterior ridges. This bone is rounded or oval in cross-section, posteriorly deeper than long; it has a cartilaginous core.

Text-figure 5.



Neostethus lankesteri, ♂. Transverse sections cutting the infrasulcar prominence, A, near its anterior end, and B, at its posterior edge, also just cutting the seminal papilla (× 18).

k., kidney; *l.*, liver; *sv.*, sinus venosus; *œ.*, œsophagus; *i.*, intestine; *u.*, ureter; *v.d.*, vas deferens; *pm.*, muscle of proctal side; *apm.*, inner muscle of aproctal side; *s.*, seminal papilla; *ip.*, infrasulcar prominence; *is.*, infrasulcar bone; *a.*, axial bone; *ct.*, ctenactinium.

The outer pulvinular bone (*pv.*) is rather similar to the inner in form and structure (Pl. III. A, *pb.*); posteriorly it bears the pointed antrorse process which appears externally as the pulvinular spine; it runs forwards outside the inner bone, but in front of the end of the latter becomes median and ventral, and extends forwards in front of the end of the axial bone to the extreme anterior end of the priapium.

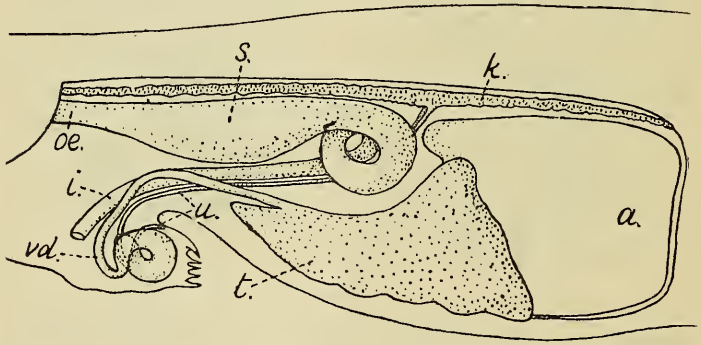
c. Viscera (text-fig. 6).

Air-bladder (*a.*), alimentary canal, kidneys (*k.*), etc., as in the female, except that the intestine (*i.*) and ureter (*u.*) end in the priapium.

The intestine (*i.*) enters the priapium near the posterior end of its junction with the body (text-fig. 5), and runs downwards, somewhat forwards, and across to the proctal side, ending at the anus.

The ureter (*u.*) enters the priapium just below and behind the intestine (text-fig. 5 B) and runs downwards into the middle of the priapium and across until it meets the enlarged part of the vas deferens, here running backwards on the proctal side; the ureter now runs upwards and backwards and towards the proctal side, always in contact with the vas deferens, and ends by opening into the efferent groove, not far from the proximal end of the latter (text-fig. 7 A).

Text-figure 6.



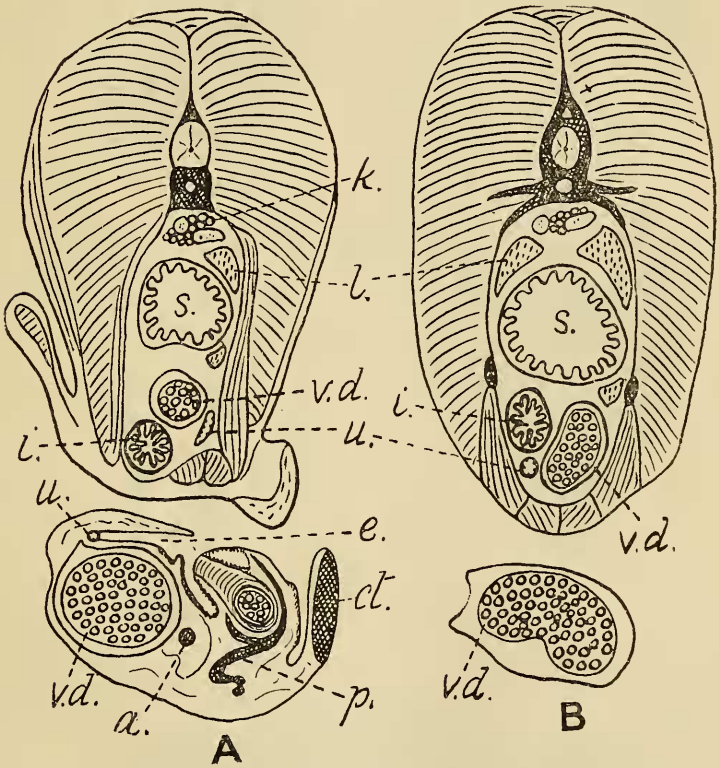
Visceral anatomy of *Neostethus lankesteri*, ♂ (× 8). From the proctal side; the liver, etc., removed.

œ., œsophagus; *s.*, stomach; *i.*, intestine; *k.*, kidney; *u.*, ureter; *t.*, testis; *vd.*, vas deferens; *a.*, air-bladder.

The testis (*t.*) is unpaired (text-fig. 8 A) and corresponds to the ovary in form and position; the vas deferens (*v.d.*) arises from the middle of the upper surface of the testis and runs forwards, at first at the side of the intestine and then partly above it; it curves downwards to enter the priapium just behind and on the aproctal side of the intestine, and runs downwards and a little backwards until it reaches the terminal style of the axial bone; the vas deferens runs across to the proctal side below this bone and then expands to form the large terminal coil that runs backwards, then across, and then upwards and forwards, ending in the seminal papilla.

The vas deferens has a thin wall, comprising an outer fibrous layer and an inner layer of mucus-secreting cells; within the testis the tubules that unite to form the vas deferens have a similar structure (Pl. IV. C). The epidermis of the glandular groove also secretes mucus, and in the neighbourhood of the seminal papilla and on the papilla itself the area of secreting-cells is increased by folding.

Text-figure 7.



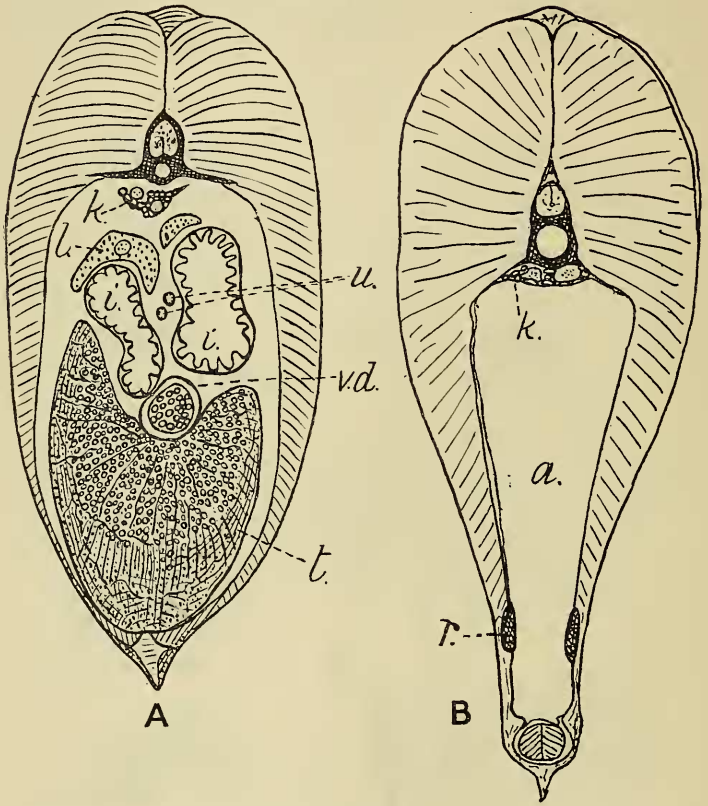
Neostethus lankesteri, ♂. Transverse sections (× 18): A, passing through the posterior part of the seminal papilla, and B, through the priapium near its posterior end.

k., kidney; *l.*, liver; *s.*, stomach; *i.*, intestine; *v.d.*, vas deferens; *u.*, ureter; *a.*, axial bone; *p.*, papillary bone; *ct.*, ctenactinium, *e.*, efferent groove.

The tubules of the testis, the vas deferens, and the glandular groove in the neighbourhood of the seminal papilla hold a mucus secretion, in which appear numerous spermatophores; these are

subspherical, with the heads of the spermatozoa at the periphery and their tails curled round inside (text-fig. 9).

Text-figure 8.



Neostethus lankesteri, ♂. Transverse sections (× 18): A, passing through testis; B, through air-bladder.

k., kidney; *l.*, liver; *i.*, intestine; *t.*, testis; *v.d.*, vas deferens; *a.*, air-bladder; *r.*, rib.

Similar spermatophores have been described in the Pœciliinæ by Philippi (Philippi, 6), but I have not been able to detect them in other Cyprinodonts.

d. Muscles (text-fig. 10).

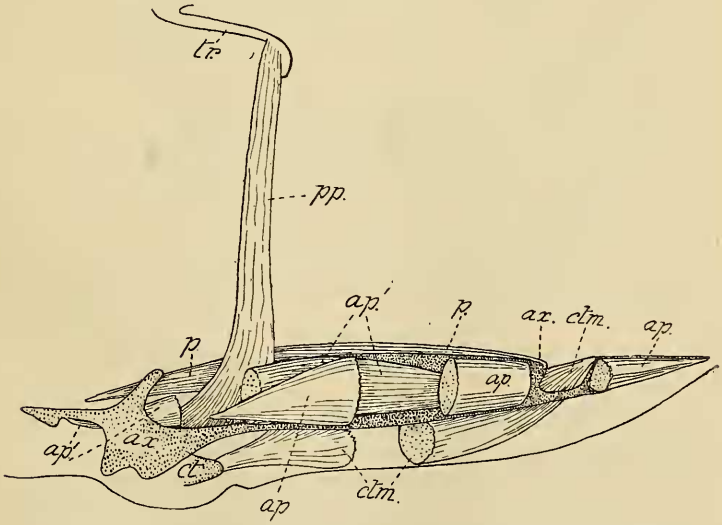
Pleuro-priapial muscle (*pp.*).—It has been mentioned that the first pair of ribs enter the priapium, and that the rib of the proctal side is much enlarged and is attached proximally to the enlarged

Text-figure 9.

Spermatophores of *Neostethus lankesteri* (× 750).

and forwardly directed transverse process (*tr.*) of the third vertebra. To this process is attached also the proximal end of a muscle that runs downwards into the priapium on the inner side

Text-figure 10.



Neostethus lankesteri. Muscles of priapium, from the aproctal side (× 20).

tr., transverse process of third vertebra; *ct.*, base of ctenactinium; *ax.*, axial bone; *pp.*, pleuro-priapial muscle; *p.*, longitudinal muscle of proctal side; *ap.*, outer, and *ap.'*, inner longitudinal muscles of aproctal side; *ctm.*, ctenactinial muscle.

of the rib, and then backwards on the proctal side of the axial bone, ending in a nodule of bone that lies near the axial bone at the level of the articulation of the ctenactinium.

Longitudinal muscles of the priapium.—These are four in number and each is more or less fusiform in shape. In front of the priapial ribs these muscles, with the intermuscular connective tissue and the axial bone, constitute the whole body of the priapium (excluding the pulvinulus) (text-fig. 4 A).

Ctenactinial muscle.—This is the largest of the longitudinal priapial muscles; it originates at the posterior end of the upper anterior ridge of the axial bone and is inserted on the proximal end of the ctenactinium. For most of its length its inner surface lies against the whole proctal face of the main crest and the lower face of the lateral ridge of the axial bone.

Outer muscle of the aproctal side.—This originates at the anterior extremity of the axial bone and runs back on the aproctal side between the anterior ridges of that bone, and then on the aproctal side of the main crest until the inner muscle intervenes; it ends posteriorly at the level of the anus in the connective tissue that lies between the floor of the glandular groove and the lateral ridge of the axial bone.

Inner muscle of the aproctal side.—Anteriorly this is inserted between the outer muscle and the main crest of the axial bone; it runs back in contact with the crest and above the lateral ridge, and then on the aproctal side of the priapial ribs, pleuro-priapial muscle, and intestine; it is attached posteriorly to the lower and proctal surface of the terminal style of the axial bone just above the vas deferens, which is here crossing to the proctal side below the axial bone.

Muscle of the proctal side.—This originates on the anterior end of the upper edge of the main crest of the axial bone, and runs backwards at first above and then at the proctal side of the ctenactinial muscle; it lies on the proctal side of the priapial ribs and intestine and behind them at the side of the inner aproctal muscle; it ends in the connective tissue that lies above the terminal style of the axial bone and between the descending portion and the enlarged terminal part of the vas deferens.

4. Neostethus bicornis, sp. n. (text-fig. 11).

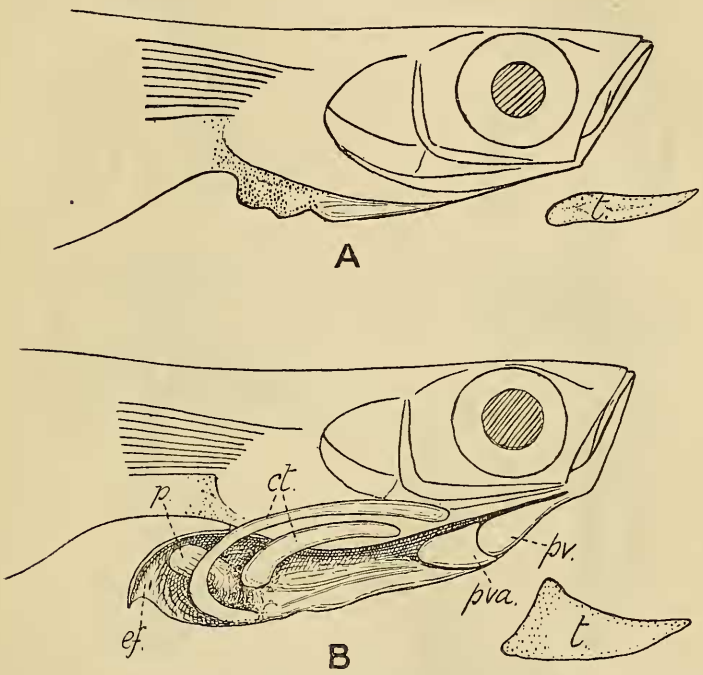
This species is more slender than *N. lankesteri* and has 36 vertebræ (16–17 + 19–20) instead of 34 or 35. There are 13 to 15 anal rays, and 35 to 37 scales in a longitudinal series.

A male of 25 mm. is not fully adult, but its priapium (text-fig. 11, B) differs from that of *N. lankesteri* in three important characters: (1) there are two ctenactinia (*ct.*), both on the aproctal side; (2) the efferent groove (*ef.*) extends downwards to the ventral surface of the posterior end of the priapium; and (3) the seminal papilla (*p.*) opens into the efferent, not the glandular groove. The ctenactinia have not attained their full

development and are cartilaginous and enclosed in skin; their final shape is uncertain; the testis (*t.*) is fairly large.

A male of 21 mm. (text-fig. 11, A) has the priapium but little developed and without trace of ctenactinia, but showing a differentiation into an anterior muscular and a posterior visceral portion; in this fish the testis is quite small.

Text-figure 11.



Neostethus bicornis: immature males; head and priapium from aproctal side (×10). Total length of fish: A, 21 mm.; B, 25 mm. The testis (*t.*) is shown separately.

pv., pulvinulus; *pva.*, pulvinular appendage; *ct.*, ctenactinia; *p.*, seminal papilla; *ef.*, efferent groove.

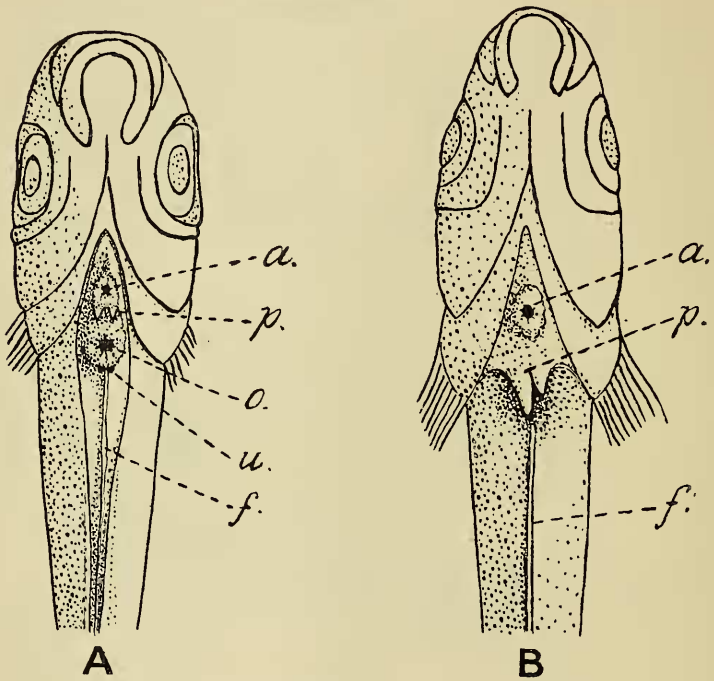
A female of 24 mm. is very similar to the female *N. lankesteri*, except for the more slender form; the postanal depression is less developed than in *N. lankesteri*, probably because the specimen is not fully adult.

The male examples are of interest as indicating that the priapium develops only as maturity approaches; presumably males, only a little smaller than the smaller one, would be almost indistinguishable from immature females.

5. *Structure of Female* PHALLOSTETHUS DUNCKERI * (text-fig. 12, A).

Total length 29 mm. The mouth is less oblique than in *Neostethus*, and the body is less compressed; the abdominal profile is not convex, but nearly straight, the rayless fringe (*f.*)

Text-figure 12.



A, *Phallostethus dunckeri*, ♀. B, *Neostethus lankesteri*, ♀. Head and abdomen from below (× 8).

a., anus; *p.*, postanal papillæ (in *Neostethus* covering the depression into which oviduct and ureter open); *o.*, opening of oviduct; *u.*, opening of ureter; *f.*, dermal fold.

lies in a groove instead of at the edge of the abdomen, and the genital opening (*o.*) does not lie in a depression; the postanal papillæ (*p.*) are minute. The dorsal fin has more rays (8 to 10)

* I have already given some account of the structure of *Phallostethus dunckeri* (Regan, **11**); the sections of the male fish are too thick and somewhat overstained, but with the much better sections of *Neostethus lankesteri* at hand for comparison I have been able to make out certain details that were difficult to see without this help. So far as I can see, the most important error in my former description was that the priapial ribs, displaced forward and separated from the vertebral column, were interpreted as elements of the pectoral arch and the antepleural bone, which embraces their ends, was not recognized as a separate bone distinct from them.

than in *Neostethus*, and the anal fin is much longer, having 26 to 28 rays. Correlated with this is the shorter abdominal region, the smaller number of præcaudal vertebræ (11 or 12), and the larger number of caudal vertebræ (26 or 27) (*cf.* Pl. I. A).

The visceral anatomy is as in *Neostethus*.

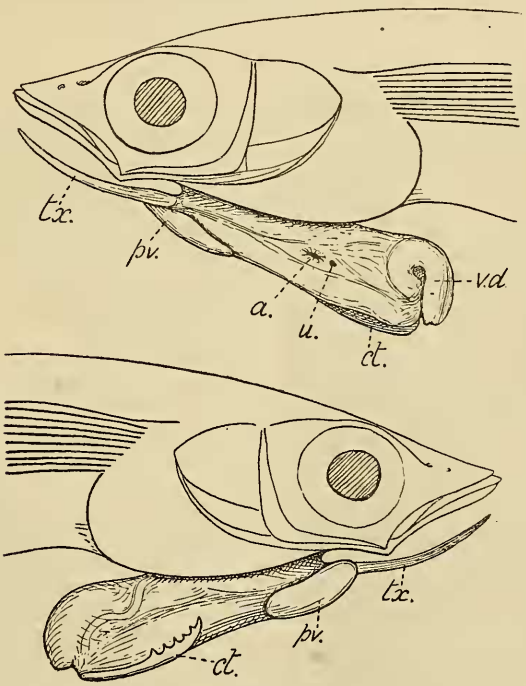
6. *Structure of Male* Phallostethus dunckeri.

In addition to the differences from *Neostethus* described above for the female, the male *Phallostethus* has many distinctive features.

a. External Characters.

Total length 25 mm. The priapium (text-fig. 13) is much more prominent than in *Neostethus*; the grooves between it and

Text-figure 13.



Phallostethus dunckeri, ♂. Head and priapium from the proctal and aproctal sides (× 10).

tx., toxactinium; *ct.*, ctenactinium; *pv.*, pulvinulus; *a.*, anus; *u.*, opening of ureter; *v.d.*, terminal coil of vas deferens.

the body of the fish are not glandular and are of equal size; they increase in depth posteriorly and meet behind the priapium to

form a median groove, which extends to the anal fin, decreasing in size backwards (text-fig. 15 B); there is no efferent groove.

The urinary opening (*u.*) is immediately behind the anus (*a.*).

The genital opening is ventral and posterior, behind the articulation of the ctenactinium (*ct.*).

The ctenactinium is short and nearly straight, with denticulated upper edge; its articulation is ventral, and it lies on the aproctal side of the priapium.

Anteriorly the attachment of the priapium to the isthmus ends at the level of the posterior edge of the eye; in front of this is a free terminal portion that ends in a second movable bony appendage, toxactinium (*tx.*); this is rounded in cross-section, tapers forwards, and curves towards the aproctal side, ending below the extremity of the lower jaw.

The pulvinulus (*pv.*) appears to be represented by a rounded shield, with thick edges, that covers the basal part of the toxactinium below and on the aproctal side.

b. Skeleton (Pl. I. A).

Third vertebra and first pair of ribs.—The transverse processes of the third vertebra are normal and symmetrical, but bear no ribs. The first pair of ribs are nearly symmetrical, but they are not articulated with the vertebral column; proximally they end at the level of the second vertebra, but at some distance from it on each side; the proximal part of the rib of the proctal side curves forwards to give attachment to the pleuro-priapial muscle. These ribs run downwards and forwards, meet below the pericardium, and enter the priapium, where they run downwards and towards the proctal side in front of the intestine.

Cleithra.—Both cleithra are prolonged forwards and enter the priapium, ending between the pulvinulus and the basal part of the toxactinium (Pl. III. B, *cl.*, *cl.'*).

Priapial skeleton.—The axial bone (text-fig. 15, *a.*) is comparatively simple; the toxactinium articulates with its anterior end superiorly and proctally (Pl. III. B, *tx.*, *a.*), the ctenactinium (text-fig. 15, *ct.*) with its posterior end inferiorly and aproctally.

The antepleural cartilage of *Neostethus* is represented by an antepleural bone that embraces the distal ends of the priapial ribs and runs forwards on the proctal side of the axial bone, ending a short distance behind the base of the toxactinium.

The pulvinulus has no pulvinular appendage and no bones; it is a ring of parenchymatous cartilage, but seems to have the structure of true hyaline cartilage in the middle (Pl. III. B, *pa.*, *pc.*).

There are no infrasulcar bones, but the terminal part of the vas deferens appears to be supported by a bony lamina, as in *Neostethus*.

c. Muscles.

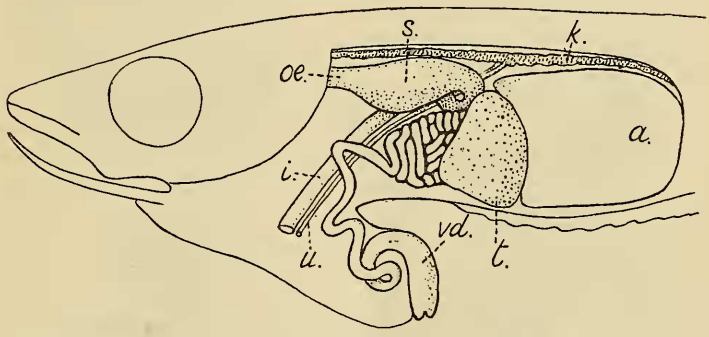
The muscles correspond to those of *Neostethus*, except that (1) the pleuro-priapial muscle is attached proximally to the

proximal part of the first rib of the proctal side instead of to the transverse process of the third vertebra; and (2) there is a toxactinial muscle (text-fig. 15, *txm.*), that lies outside the longitudinal muscle of the proctal side, ends posteriorly between the coils of the vas deferens, and anteriorly is inserted on the base of the toxactinium.

d. Viscera (text-fig. 14).

A difference from *Neostethus* is that the ureter (*u.*) accompanies the intestine (*i.*) and opens behind the anus; of more importance are differences in the testis and vas deferens (*vd.*). The testis (Pl. IV. A) has no tubules lined with a distinct epithelium, even near the origin of the vas deferens, which leaves the testis (*t.*) anteriorly and at once becomes coiled up into a mass that lies in front of and to the right side of the testis; this "epididymis" is similar to the testis in form and is not much less than it in size

Text-figure 14.



Visceral anatomy of *Phallostethus dunckeri*, ♂; the liver, etc., removed (× 10).

œ., œsophagus; *s.*, stomach; *i.*, intestine; *k.*, kidney; *u.*, ureter; *t.*, testis; *v.d.*, vas deferens; *a.*, air-bladder.

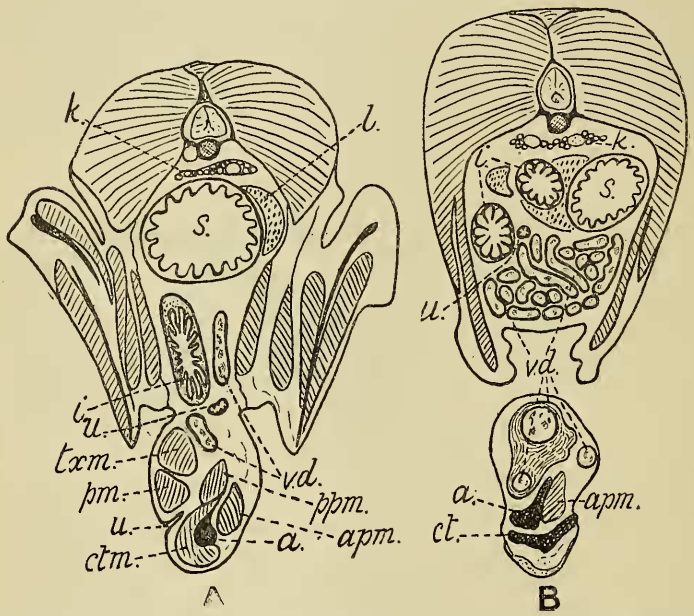
(text-fig. 15, B); the vas deferens emerges from its narrowed anterior end, enters the priapium, and runs backwards on the aproctal side to above the base of the ctenactinium, then across to the proctal side before coiling round in a complete circle and opening ventrally to the exterior in a short seminal papilla behind the base of the ctenactinium.

The vas deferens is lined with a glandular epithelium; in the "epididymis" this is formed of long columnar cells with basal nuclei (Pl. IV. B). The outer fibrous layer is quite thin, except in the terminal coil, where it is thick. The lumen contains spermatozoa, which seem to adhere together, their heads forming more or less convex plates, whilst their tails are dependent from the concave surfaces. However, this structure cannot be very definitely made out from the sections, but it seems clear that there are no spermatophores of the type described in *Neostethus*.

7. *Remarks on the Structure of the Priapium.*

Many of the peculiarities of the priapium of *Phallostethus*, as compared with that of *Neostethus*, seem connected with the two main differences, that the vas deferens opens directly to the exterior instead of into a glandular groove and that a toxactinium is present. To the absence of a glandular groove may be due the great length of the vas deferens, which coils to form an "epididymis"; the secretion supplied in *Neostethus* by the testis,

Text-figure 15.



Phallostethus dunckeri, ♂. Transverse sections (× 18): A, showing the intestine, vas deferens, and ureter entering the priapium, and also the ureter opening to the exterior; B, showing the "epididymis" and the posterior thick-walled portion of the vas deferens above the articulation of the ctenactinium.

k., kidney; *l.*, liver; *s.*, stomach; *i.*, intestine; *u.*, ureter; *v.d.*, vas deferens; *a.*, axial bone; *ct.*, ctenactinium; *ppm.*, pleuro-priapial muscle; *txm.*, toxactinial muscle; *ctm.*, ctenactinial muscle; *pm.*, muscle of the proctal side; *apm.*, inner muscle of the aproctal side.

the vas deferens, and the glandular groove comes in *Phallostethus* from the vas deferens alone. The efferent groove, infrasulcar bones, and pulvinular appendage of *Neostethus* are all directly connected with the glandular groove, and it is not surprising that they are absent in *Phallostethus*.

The approximate symmetry of the priapial ribs and cleithra in *Phallostethus*, as compared with their marked asymmetry in *Neostethus*, is no doubt due to the symmetrical attachment of the priapium in the former (text-fig. 15), and its asymmetrical attachment, owing to the great development of the glandular groove, in the latter (text-fig. 4).

With the presence of a toxactinium as a free appendage may be correlated the freedom of the anterior part of the priapium in *Phallostethus*, whereas in *Neostethus* it is attached to the isthmus right to the end. It seems probable that the toxactinium may replace functionally the anterior part of the ctenactinium of *Neostethus*, and that the shortness of the ctenactinium of *Phallostethus* may be connected with this.

In both genera the ureter enters the priapium and runs downwards and across to the proctal side behind the intestine; in *Phallostethus* it opens to the exterior just behind the anus, but in *Neostethus*, owing to the shortness of the free posterior part of the priapium and the great size of the terminal coil of the vas deferens, it finds the latter in its way and has to surmount it before reaching the surface at some distance from the anus.

In *Phallostethus*, as compared with *Neostethus*, the great length and coiling of the vas deferens, the separation of the first pair of ribs from the vertebral column, and perhaps the presence of a toxactinium, may be features of specialization; in *Neostethus* the development of the glandular groove and the structures associated with it may be similarly regarded.

When I first described *Phallostethus* I suggested that the axial bone of the priapium might be pelvic and the ctenactinium and toxactinium fin-rays. This interpretation seems much less likely to be correct when the structure of *Neostethus* is considered also. The antepleural cartilage of *Neostethus* has developed in *Phallostethus* into a long bone with a cartilaginous core; conversely, the presence in *Neostethus* of pulvinular and infrasulcar bones, absent from *Phallostethus*, seems to show that the skeletal elements of the priapium develop when and where they are wanted, and are not to be homologized with any other parts of the skeleton. Moreover, the pulvinular appendage of *Neostethus* seems to represent a stage of development intermediate between a simple dermal papilla and movable bony appendages, such as the ctenactinium and toxactinium, and suggests that these may have originated as outgrowths whose skeleton changed from connective tissue to cartilage and then to bone as they grew longer and formed more definite proximal articulations with the axial bone. Their development in *Neostethus bicornis* supports this view.

In fact, the whole priapium seems to be an entirely new formation; its appendages, bones, muscles, and glands are not to be homologized with any structures found in the female fish or in other Cyprinodonts.

8. *Use of the Priapium.*

In oviparous Cyprinodonts (*Fundulus* and *Cyprinodon*), Newman (5) has observed the intercourse of the sexes; the male and female lie side by side and looking in the same direction, and the male clasps his mate by folding his dorsal and anal fins across her, whilst the paired fins also may interlock; in this way the eggs and sperm are extruded in such close proximity that fertilization is assured.

It seems likely that in the Phallostethinæ also the male and female take up a similar position, the female lying on the aproctal side of her mate.

In *Phallostethus* the toxactinium, which curves towards the aproctal side, may grip her under the chin or even be held in her mouth, whilst the serrated edge of the ctenactinium may give it a firm hold on the pectoral region in front of and on the far side of the genital orifice, in order that the seminal papilla may be placed against or introduced into the latter.

In *Neostethus* in seems likely that during intercourse the female may be held by the ctenactinium across the back of the head, the anterior descending part lying on her distal side and the terminal part that at rest curves across under the chin of the male now curving towards him, perhaps under hers. The spinous process of the ctenactinium and the pulvinular spine would stick into her on the side near the male. The posterior end of the priapium may be held in the depression into which the oviduct opens, whilst the terminal projecting part of the fold that roofs the efferent groove and the membranous fringe below it may form a sort of tube for insertion into the genital aperture of the female.

The asymmetry of the postanal papillæ of the female may be due to the side by side position presumably adopted; if so, it may be supposed that a male with the right side aproctal would pair with a female that had the smaller papilla on the left side, and *vice versâ*.

It is possible that no part of the priapium is actually introduced into the oviduct, and that the spermatophores, first discharged into the glandular groove and then ejected through the efferent groove, may adhere to the surface of the postanal papillæ and of the depression into which the oviduct opens, and that they may be introduced into the oviduct by the action of the papillæ.

The infrasulcar prominence may prevent the flow of the seminal fluid outwards or forwards at the place where it exerts the greatest pressure, and the pulvinular appendage may possibly help to drive the glandular secretion backwards.

In both *Phallostethus* and *Neostethus* the probable effect of the contraction of the longitudinal muscles of the aproctal side and of the pleuro-priapial muscle would be to move the posterior end of the priapium aproctally; an additional effect in *Neostethus* would be to close the glandular groove.

It is only by a study of the actual behaviour of these fishes during the breeding-season that one can hope fully to understand the purpose for which this elaborate apparatus has been evolved.

9. *Comparison of the Priapium with other Copulatory Organs of Fishes.*

In many bony fishes a papilla bearing the genital aperture forms a simple but efficient intromittent organ; in others the anal fin is utilized, the vas deferens either opening at its base or being prolonged on the fin, which may form a copulatory organ of considerable complexity of structure, as in the viviparous Cyprinodonts, Pœciliinæ, Anablepinæ, etc. (Regan, **10**; Garman, **1**; Langer, **4**).

In its asymmetry and in being either dextral or sinistral the priapium agrees with the copulatory organ of *Anableps* (Garman, **1**).

In the Phallostethinæ the remoteness of the genital opening from the anal fin explains why the latter has not been involved, but does not explain the extraordinary complexity of the priapium, which parallels the mixopterygia of the Selachians in its specialized skeletal and muscular system (Jungersen, **3**).

In the mixopterygia new skeletal elements are developed, and may either margin a groove or may become movably articulated with the main axial piece; one may project as an external spine, in this case formed of calcified cartilage, not of bone. Another parallel with the priapium is that the mixopterygia attain their full development rapidly as the individual becomes sexually mature.

In the Selachians the mixopterygium has a nearly uniform structure in members of the same family, or even of the same suborder (Huber, **2**; Regan **7**), and the differences between the priapia of *Phallostethus* and *Neostethus* are as great as between the mixopterygia of the subclasses Holocephali and Euselachii.

10. *Rank and Position of the Phallostethinæ.*

There can be little doubt but that *Neostethus* and *Phallostethus* belong to the family Cyprinodontidæ, and they seem to agree in every way with the most generalized subfamily, the Fundulinæ, except for three features of specialization, namely, the anterior position of the anus, the absence of pelvic fins, and the development of a priapium in the male. This view as to their relationship is best expressed by placing them in a distinct subfamily, Phallostethinæ, of the Cyprinodontidæ, a family that already includes both oviparous and viviparous fishes, the latter with intromittent organs of three different types (Regan, **8**).

Other examples of animals which retain the general structure of the group to which they belong, whilst one particular organ or system is profoundly modified or some new feature of importance

is developed, can readily be found, although few cases are so striking as the Phallostethinæ.

Among fishes, one may recall the curious Cyprinid *Gyrinochilus* (Regan, 9, p. 29), which has the form, fins, scales, etc., of *Crossochilus* and *Discognathus*, to which it is certainly closely related, yet it has the mouth, gills, and pharyngeals so modified in connection with its peculiar methods of breathing and feeding that some ichthyologists have regarded it as the type of a separate family.

Because *Neostethus* and *Phallostethus* so obviously belong to the large and varied family Cyprinodontidæ, one attaches but little classificatory importance to the development of the priapium and its evolution along two very distinct lines. But if these were the only known Cyprinodonts they would certainly form a separate order, and the differences in structure of the priapia would be regarded not merely as generic, but as subordinal, and the much longer anal fin, the abdominal groove, etc., of *Phallostethus* would be held to support the view derived from the structure of the priapia that it and *Neostethus* had diverged widely and through a long period of time from their common ancestor.

Were these the only living Teleosts many zoologists would regard them as a separate class, comprising two well-marked orders, just as some have suggested that the Dipnoans should be removed from the Pisces, mainly on account of the isolated position of their living representatives, *Ceratodus* and the Lepidosirenidæ, and have given these ordinal rank with the names Monopneumones and Dipneumones.

These somewhat fanciful considerations are put forward merely to suggest that the rank given to a group depends on several factors, and that the degree of differentiation is one of the least of these.

11. *Note on the Origin and Homologies of Skeletal Elements.*

The priapium appears to be an entirely new organ, and it has a highly developed skeleton, comprising a number of new elements that cannot be homologized with any parts of the skeleton of other fishes; this suggests that the intermuscular connective-tissue may give rise to cartilaginous or bony elements whenever and wherever the necessity may arise. This is, of course, not new, but it is a point of view not always kept in mind by morphologists, as could be illustrated by numerous examples, one of which may be adduced.

In certain Selachians, and especially in the Hypotremata, there is a median series of vertical cartilaginous plates above the vertebral column, and the question has been raised whether these belong to the vertebral column or to the fin-skeleton. Thus Goodrich (Lankester's 'Treatise of Zoology,' pt. ix. figs. 50, 52) has figured them in *Squalus* and *Squatina*, and has described them as either modified radials or neural spines. I have long thought it probable that they were neither, but autogenous

structures developed in the intermuscular septum, and I feel this opinion strengthened as the result of my work on the Phallostethinæ.

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EXPLANATION OF THE PLATES.

Plate I.

Skeletons of *Phallostethus dunckeri* (A) and *Neostethus lankesteri* (B), reconstructed; A 6 and B 5 times the actual size.

Plate II.

Neostethus lankesteri.

A. Transverse section through anterior part of seminal papilla and adjacent portion of glandular groove (× 130). *e.*, glandular epidermis lining folds and pockets on surface of papilla; *p.*, papillary bone; *sp.*, mass of mucus containing spermatophores, lying in the vas deferens, where this opens into the glandular groove (*g.*); *a.*, process of axial bone.

B. Transverse section through glandular groove and pulvinulus at base of pulvinular appendage (× 130). *g.*, glandular groove; *i.*, infrapulvinular groove; *is.*, anterior infrasulcar bone; *pvb.*, cartilaginous terminal process of inner pulvinular bone, for articulation of pulvinular appendage (*pva.*).

Plate III.

A. *Neostethus lankesteri.* Transverse section through isthmus and anterior part of priapium (× 130); the right side is aproctal. *u.*, urohyal; *cl.*, cleithrum of aproctal side; *a.*, axial bone; *pb.*, outer pulvinular bone; *g.*, glandular epidermis; *m.*, outer muscle of aproctal side.

B. *Phallostethus dunckeri.* Transverse section through isthmus and anterior part of priapium, showing the toxactinium articulating with the axial bone (× 130); the left side is aproctal. *u.*, urohyal; *a.*, axial bone; *tx.*, toxactinium; *cl.*, *cl.'*, cleithra; *pc.*, pulvinular cartilage; *pa.*, parenchymatous cartilage.

Plate IV.

A. *Phallostethus dunckeri.* Transverse section through part of testis near origin of vas deferens (× 200).

B. *Phallostethus dunckeri.* Transverse section through "epididymis" (× 170).

C. *Neostethus lankesteri.* Transverse section through upper part of testis (× 170).